THE REACTIONS OF AMPHIBIANS TO LIGHT.

By A. S. Pearse.

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TABLE OF CONTENTS.

I. INTRODUCTION.

A. HISTORICAL.

CONSIDERABLE interest has lately centred itself in the study of the behavior of animals under the influence of light, and the results of such studies have been largely used in formulating the various theories which attempt to account for the reactions of organisms after they have been subjected to external stimulation. Among vertebrates the amphibians offer particularly favorable material for such study, as the various species may be used for experimentation in or out of the water; they are, as a rule, very responsive to photic stimulation and are able to withstand severe operations without serious interference with their reactions. A large amount of work by a number of observers has already been done in the study of light responsiveness, and in the next few pages an attempt is made to summarize the results of those studies, so far as they apply to amphibians. For the sake of clearness this material will be considered from a comparative standpoint rather than in an historical order.

Amphibians react to light by giving motor responses. This motor reaction to illumination was first recorded by Configliachi and Rusconi ('19).[1] They observed that Porteus anguinus, the blind cave salamander of Europe, became restless when exposed to light, and this observation has been confirmed by later observers (Semper, '81; Dubois, '90; Beer, :01).[1] Since that time responsiveness to light has been noted in the following genera: Triturus, or Triton (Graber, '83, '84; Willem, '91), Necturus (Cope, '89, Reese, :06), Cryptobranchus (Reese, :06, B. G. Smith, :07), Diemyctylus (Jordan, '93), Spelerpes (Banta and McAtee, :06), Rana (Kühne, '78ᵃ; Loeb, '90; Parker, :03ᵇ; Torelle, :03, Yerkes, :03, :06; Dickerson, :06; Holmes, :06; Cole, :07), Acris

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[1] The numbers in parentheses indicate the year of publication of the article referred to, the title of which is given in full in the "Bibliography" at the end of the paper. An apostrophe indicates an omitted 18; a colon, an omitted 19.

(Cole, :07), Bufo (Graber, '84).   As these are representative genera, it seems evident that photic stimulation exerts an influence of wide range among the amphibians.

Many amphibians show a marked tendency to orient the body and to move toward or away from the source of light.   Configliachi and Rusconi ('19) observed that Proteus tended to go to the side of an enclosure farther from the light and remain there.   Since then a number of observations have been made concerning the phototropism of amphibians. Thus, the following have been claimed to be positively phototropic: Rana sp. ? (Holmes, :06 ; Dickerson, :06), R. temporaria (Plateau, '89), R. clamata (Torelle, :03 ; Yerkes, :03, :06 ; Cole, :07), R. pipiens (Parker, :03^b ; Torelle, :03), Acris gryllus (Cole, :07), Bufo clamita (Plateau, '89) ; and the five following negatively phototropic: Proteus anguinus (Configliachi and Rusconi, '19; Dubois, '90), Necturus (Cope, '89 ; Reese, :06 ; B. G. Smith, :07), Spelerpes maculicaudus (Banta and McAtee, :06), Rana (Loeb, '90).   It will be seen from this list that the photic reactions of the Caudata are negative, while those of the Salientia are positive, with the exception of the observations by Loeb ('90), which do not agree with those of other writers.

Some amphibians show a tendency to come to rest in the shade.   We would perhaps expect such a reaction in species which are normally negative in their phototropism, but Torelle (:03) has shown that the frog, which is strongly positive, will also go toward a shaded area and come to rest in it, though the animal then faces toward the light. Graber ('83, '84) had previously found that Triturus, Rana, and Bufo tended to come to rest in shadow.

The eyes are not essential for the light reactions, that is, such reactions may be brought about by stimulation through the skin.   Configliachi and Rusconi ('19) ascribed the photic reactions of Proteus to the painful effect of light upon the skin, but Kohl ('95) showed that, while the eyes of this species are rudimentary, they might nevertheless be effective photoreceptors.   It remained for Dubois ('90) to show that the reactions of Proteus might take place through the skin alone.   He blackened the eyes and obtained a reaction from an individual in which only the tip of the tail was illuminated.   Graber ('83, '84) observed reactions in Triturus, which were like those of normal individuals, after the eyes had been removed and the orbits filled with black wax.   More recently Parker (:03^b) has shown that Rana is positively phototropic with and without the eyes ; and Cole (:07), besides corroborating Parker's observations, has obtained like results from Acris.   Korányi ('93) observed reflex leg movements in a frog, which had been rendered particularly sensitive by treating the brain

with meat extract, when he threw a strong beam of light on its back. Reese (:06) found that when only the tip of the tail was illuminated in Cryptobranchus or Necturus, the individuals thus stimulated moved out of the lighted area.

The reactions brought about by stimulating the eye alone agree, in kind, with those brought about through the skin. Parker (:03^b) found that frogs in which the skin was covered but the eyes were exposed, were positively phototropic, like individuals in which the eyes had been removed. Torelle (:03) made an observation which bears indirectly on the same point. She found that frogs which had one eye covered with black cambric went toward the light at an angle or made circus movements with the uncovered eye towards the centre.

The positive phototropism of amphibians is apparently a reaction toward a greater intensity of illumination; or, with the eyes, toward a greater illuminated area. Plateau ('89, p. 88) observed that Rana and Bufo, when placed in a box having two openings, went toward the larger aperture even though it was covered with a grating. Cole (:07) showed that when Acris was placed between two lights of the same quality and intensity but of different areas, it went toward the larger area, but when individuals in which the optic nerves had been cut were placed in the same situation, they went toward either light an approximately equal number of times. Rana also showed the same reaction toward the larger area when it was in normal condition. Torelle (:03) found that the direction of the illumination made no difference in photic responses, as frogs went toward the lighter end of a box when the illumination was from below, and Reese (:06) has made similar observations on Cryptobranchus and Necturus. Dickerson (:06, p. 32) says, "Frogs do not distinguish between a lighted space and a white solid. They will turn toward a white card or paper and try to jump through it, and they may struggle at the impossible task of working their way into the solid white surface made by the leaf edges of a closed book."

Torelle(:03) noted that frogs, when they were confined in a small space with an opening above, pointed the head upward toward the opening, and she supposed this to be evidence for the directive action of the rays. Objection may be made to this view on the ground that the opening offers the only opportunity for escape, and the animal, seeing the opening with its eyes, points its head toward it. If she had shown the same reaction with eyeless individuals, the evidence would have been more conclusive.

The rays toward the violet end of the spectrum are apparently most potent in producing photic reactions, and the rays toward the opposite

end approach in their effects the conditions brought about by dark.
Graber ('83, '84) found that Triturus did not come to rest in the colors
toward the violet end of the spectrum when there was equal oppor-
tunity to remain in those nearer the opposite end.   This was true of
blinded as well as normal animals.   He also ('84) found that Rana
and Bufo reacted in much the same way.   He states that his results
could not have been due to the effect of temperature, as he performed
experiments in which he used a heat screen for the blue and none for
the red light, and the results were the same.   Kühne ('78ª) had pre-
viously observed that normal frogs went from green toward blue light,
while blinded individuals did not.   Loeb ('90) states that the less re-
frangible rays do not affect light reactions to such an extent as those
of greater refrangibility, and in this connection he remarks that a frog
will jump towards a red cloth.   (He found Rana to be negatively pho-
totropic.)   Torelle (:03) in speaking of the frog recorded in a stronger
positive phototropism for blue light than for red, yellow, or green ; and
this was the same when the light was reflected, transmitted, or both.
The individuals she used were indifferent to red light.   Reese (:06)
found blue to be most potent in causing reactions in Necturus and
Cryptobranchus.   Yerkes (:03, p. 586) suggested that the frog might
be able to distinguish between red and white backgrounds, but, as he
says (:06, p. 548), there is nothing to show that these reactions might
not have been due to intensity differences.   Holmes (:06, p. 350) in
speaking of frogs sums up the whole matter by stating that " in general
it may be said that where they are able to go toward one of two colors,
of equal intensity, they move to the color lying nearest the violet end
of the spectrum."

*The phototropic reactions of amphibia are apparently not due to the
direct stimulation of the central nervous system by light.*   Parker (:03ᵇ)
found that eyeless frogs responded positively when only the lower part of
the body was illuminated from the side in such a manner that the central
nervous organs were in shadow.   The experiments of Dubois (:90) on
blinded Proteus, and Reese (:06) on Cryptobranchus and Necturus
offer additional evidence on this point.   These animals reacted to a
beam of light thrown on the tail, and hence beyond the limits of the
central nervous organs.

*Various internal and external factors may influence the responses of
amphibians to light.*   It is probable that there are many factors which
exert such a modifying influence.   Those which are enumerated in the
following paragraphs are known to alter the photic responses of certain
amphibians by producing changes in their physiological states.

Breeding season.   Jordan (:93, p. 271), in speaking of Diemyctylus,

says they "usually conceal themselves under fallen leaves and among the tangle of water weeds. On warm, sunny days in early spring, however, they bask openly in the sunshine along the shore." Another instance is given by B. G. Smith, (:07, p. 6), who remarks that "Cryptobronchus comes forth but seldom in the daytime except during the breeding season," and (p. 32) "with the close of the breeding season, becomes more shy, avoids the light and is seldom seen in the open."

Temperature. Torelle (:03, p. 475) stated that the positive phototropism of the frog increased as the temperature was raised. If, however, the temperature rose above 30° C., these animals were indifferent to light, and if it fell below 8° C., they became negative. Cole (:07, p. 401) has shown conclusively that conditions of temperature influence the photic responses in Rana. As has been stated, his method was to place the animals between two lights of equal intensities but different areas. When a frog has been cooled to from 6° to 10° C., it went toward the smaller illuminated area, but after it became warm its reactions were uniformly toward the larger area.

Previous photic stimulation. Configliachi and Rusconi (:19) noticed that after Proteus had been exposed to light for some time, its reactiveness to that stimulus decreased. Reese (:06, p. 94), in experimenting with Cryptobranchus and Necturus, found that "the responses to light were much more marked for the first ten or a dozen stimulations." Torelle (:03, p. 47), on the other hand, observed that, after five to eight hours' exposure to light, frogs exhibited the same positive phototropism as before.

Stereotropism. Eigenmann and Denny (:00, p. 34) in speaking of Typhlotriton, say that "it seems probable that sterotropism rather than negative heliotropism accounts for the presence of this species in caves." Torelle (:03, p. 477) found that Rana was strongly stereotropic below 8° C. This stereotropism was associated with a change from positive to negative phototropism, and, as Holmes (:06, p. 349) has pointed out, may have been responsible for such change.

Age. Banta and McAtee (:06, p. 71) in their experiments with the cave salamander found that "all larvæ are very much more responsive to light stimulus than the adults, the young larvæ more so than the older."

Surrounding medium. Torelle (:03, p. 473) has shown that frogs will go toward the light under water as well as in air. The change in surrounding medium, and from walking to swimming, apparently does not alter the reactions.

B. METHODS.

The experiments described in the present paper have been devoted (1) to extending the range of our knowledge of photic reactions among the amphibians, (2) to ascertaining more fully the nature of the photo-receptors involved, and (3) to determining how great a part the central nervous system takes in these reactions. It gives me great satisfaction to express my indebtedness to Professor G. H. Parker, under whose direction the work was accomplished.

All the experiments which are described in the succeeding pages were carried on in a dark room, the temperature of which usually varied between 17° C. and 21° C. The source of the light was a six-glower Nernst lamp, and as the amount of light it gave out varied under different conditions, the intensity used is given under the descriptions of the various experiments. All the amphibians used were collected in the vicinity of Cambridge, Massachusetts, with the exception of Necturus, which came from Venice, Ohio; Cryptobranchus from Oil City, Pennsylvania, and, through the kindness of Professor A. M. Banta, from Marietta, Ohio; and Diemyctylus from Jaffrey, New Hampshire. The aquatic species were kept in a large aquarium tank, four meters long by one and a half wide, in a cool basement room. The terrestrial forms were kept in cages, the floors of which were covered with earth and dead leaves, and individuals upon which operations had been performed were placed on a bed of moist excelsior in glass jars. Little trouble was experienced in keeping the animals in good condition. The frogs and toads were fed with meal worms, which they ate readily throughout the winter. The other species were not fed, though Cryptobranchus may have eaten frogs, which were kept for other purposes in the aquarium with it; and as one of those animals lived for two years, it is not improbable that it obtained such food from time to time. The experiments were carried out in the autumn and winter months (October 1 to April 1) of two different years.

Of the aquatic species used, Cryptobranchus was the most reactive. For experimental purposes Bufo was the most satisfactory of the land forms, both on account of its extreme activity and its greater ability to withstand dryness. Both Bufo fowleri and B. americanus were used, but the experiments on the two species were not kept separate. Dr. L. J. Cole informs me that Acris is much better than Bufo for work of this nature, but I have not had an opportunity to try it. The term "amphibians" in this paper does not include caecilians, whose reactions to light are, so far as I know, unstudied.

II. OBSERVATIONS.

A. The Photic Reactions of Normal Amphibians compared with those from which the Eyes have been removed.

In order to compare the reactions of amphibians in which both the skin and eyes acted as photoreceptors with those in which only the skin was open to stimulation, individuals were tested both in normal condition and after the eyes had been excised. The eyes were usually removed by making a single transverse cut as near the anterior edge of the ear drums as possible. The whole front of the head, including the olfactory lobes and a part of the cerebral hemispheres, was removed by this method of procedure (Figure 1). In Necturus and Cryptobranchus, however, only the eyes were excised. All the species stood the operation well and subsequently gave typical reactions, except Plethodon and Diemyctylus, which were apparently much weakened by it and were indifferent to light after the eyes had been removed. As a rule individuals were not used for experimentation until the day after the operation.
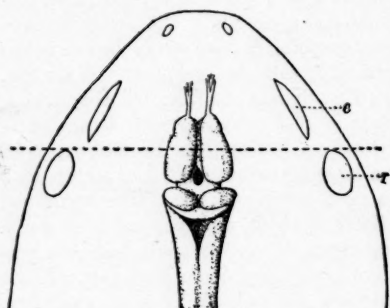
FIGURE 1. Dorsal view of toad's head showing the position of the brain. The dotted line indicates the plane of the cut used in removing the eyes. e, eye; r, ear.

The species studied fall naturally into two groups, aquatic and terrestrial. The former group included Necturus maculosus and Cryptobranchus alleghiniensis, and the terrestrial species studied were Amblystoma punctatum, Plethodon cinereus, Diemyctylus viridescens, Rana clamata, R. sylvatica, Bufo fowleri, and B. americanus. The reactions of each species will be considered separately.

(a) Necturus maculosus.

The first experiments with this species were intended to show what influence light had upon its movements. Four individuals were placed successively in the centre of a large aquarium, which was illu-

minated from one end in such a way that the light had an intensity of about 220 candle-meters at its centre. Under these conditions an individual usually went at once to the end of the aquarium farther from the light. It then wandered about from one end to the other for some time, but finally came to rest as far as possible from the light. If the lamp was then changed to the opposite end of the aquarium, the animal again moved to the end which was farther from the light and came to rest.

In order to test the reactions of Necturus to light and shadow, the lamp was moved to the side of the aquarium and a movable screen interposed in such a way that one half of the aquarium was in shadow and the other half in light (220 candle-meters at the centre of the aquarium). Two animals were successively introduced. One of these, after wandering back and forth from one end to the other, came to rest in the shaded end of the aquarium. When the screen was changed to the opposite half, the animal moved again into the shaded area, and this action was repeated for five successive trials on two different occasions. The other individual remained at the side of the aquarium nearer the light, and in two experiments it kept going back and forth from light to shadow for more than one hour. It apparently did not avoid the light, but, by comparing the time it spent in the light with that spent in shadow during half an hour, it was found that three-fifths of that period had been passed in the shaded part of the aquarium. The first individual, then, invariably came to rest in the shadow, and the second one, while it continued to move actively, spent somewhat less time in the light than in the shadow.

The most decisive reactions shown by Necturus were brought about by illuminating a small area at its anterior or posterior end. The apparatus was in the same position as for the experiments just described, except that a screen was arranged in such a manner that a vertical band of light about five centimeters wide could be suddenly thrown on different regions of the body. Four individuals were used for these experiments and all of them behaved in essentially the same manner. After an animal had remained quiet in the dark for five minutes, it was suddenly illuminated, and a reaction usually took place within a few seconds. When the light fell on the tail, the animal moved forward, but when it was allowed to fall on the head, the movement was usually backward. Since the animals were never tested with the light until they had been quiet in the dark for five minutes, these reactions were without doubt due to the illumination, for they took place within a few seconds of the time when the light was thrown on the animals.

In order to discover whether the skin of Necturus was sensitive to light or not, the eyes were removed from two individuals and they were then tested by local stimulation as described in the last paragraph. Their reactions were similar to those of animals with eyes except in one particular. The average time which elapsed before the individuals with eyes moved out of the lighted area was shorter when the head was stimulated than when the light fell upon the tail, but the eyeless animals, on the contrary, reacted more quickly when the tail was stimulated. The results with normal animals agree with those of Reese (: 06, p. 96) in his experiments on Necturus. He ascribed the shorter reaction time for the head to greater sensitiveness in that region, and he believed it to be due to stimulation received through the eyes. The present experiments with eyeless animals give support to his views, as the posterior end of the individuals tested was apparently more sensitive to photic stimulation after the eyes had been excised. The decreased sensitiveness of the head region may, however, have been due to the injury incident to the removal of the eyes, instead of the mere loss of the eyes themselves.

From the experiments described it is evident that Necturus is negatively phototropic and that it comes to rest in shaded areas. Both the skin and eyes act as photoreceptors, and the stimulation of either brings about negative reactions.

(b) Cryptobranchus allegheniensis.

The arrangement of the apparatus for the experiments with Cryptobranchus was the same as for those with Necturus. The reactiveness of this species to light was very marked. Seven individuals were placed successively in the middle of the aquarium, the illumination being from one end, whereupon they moved immediately to the end farther from the light. When the lamp was carried to the opposite end of the aquarium, they usually changed their position at once and again came to rest in the end farther from the light. In these reactions they were much more responsive than Necturus, though, as Reese (: 06, p. 94) has observed, they often failed to respond readily after the first few reactions.

The reactions of Cryptobranchus to conditions of light and shadow were also pronounced. In testing these, half the aquarium was shaded by a screen which was changed from one end to the other at five minute intervals. An individual was placed in the aquarium and the screen changed ten times. It never failed to move at once to the shaded part of the aquarium, and furthermore it rested quietly in the shadow in the intervals between the changes.

The illumination of a small area at the anterior or posterior end of an individual produced the same reactions as in Necturus, but in Cryptobranchus they took place more quickly.

To test the sensitiveness of the skin to light, the eyes were removed from one individual and it was stimulated alternately on the head and tail by the same method as that used for Necturus. This animal usually responded within a few seconds to such illumination. In a series of fifty reactions it was found that the average time required for the animal to move out of the illuminated area was more than twice as great when the light fell upon the head as when the tail was illuminated in the same manner. The skin of Cryptobranchus is, then, a photoreceptor and the sensitiveness seems to be greater at the posterior than at the anterior end. Reese (:06, p. 94) has stated that, even with the eyes present, this species shows the greatest sensitiveness to light in the caudal region.

This eyeless individual was strongly photokinetic. It was placed in a flat porcelain dish about a meter below an ordinary gas burner, and after it had been allowed to remain in the dark for about an hour, the gas was suddenly lighted. There was an unfailing response to this illumination within a few seconds, the animal moving restlessly about in the dish. As the light was non-directive, and the animal often remained quiet for hours in the dark, this uniform response to sudden illumination showed this species to be strongly photokinetic. In this respect it was quite different from Necturus, which often did not respond to such stimulation for some time, even when the light intensity was 220 candle-meters.

In summarizing the results of the experiments upon Cryptobranchus, it may be said that it is negatively phototropic, that it comes to rest in shaded areas and is strongly photokinetic. These reactions apparently take place as readily when only the skin is stimulated by light as when the eyes are also affected.

The terrestrial amphibians were found to be much more satisfactory subjects for experimental work than the aquatic species. Not only was it easier to arrange the apparatus for the land forms, but more accurate results were obtained, as it was possible to orient the animals with a perfectly uniform relation to the light before each reaction. In all the experiments with terrestrial forms the apparatus shown in Figure 2 was used. After this apparatus had once been arranged, it was a simple matter to test one species after another, and to compare the reactions of normal animals with those of individuals without eyes. It will be seen from the figure that the two side screens (s′) were placed

at the edge of the shadow made by the light that passed through the
heat screen (a). Thus the greatest open space was away from the
light, and, as far as the animal was able to see, the best chance for
escape lay in that direction. An individual was not, then, subjected to
the same conditions as one placed in a small box having a single
opening. It does not seem improbable that any animal with eyes,
after being handled and shut up in a small enclosure, would endeavor
to escape by the most apparent opening; and the reactions could not ·
in that case be interpreted as being due to the influence of light alone.
The apparatus shown in Figure 2 is not open to such an objection.
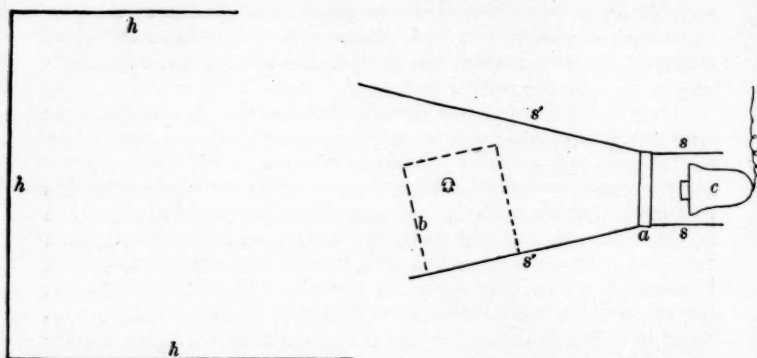
FIGURE 2. Plan of apparatus in which the reactions of terrestrial amphib-
ians to light were tested. a, heat screen filled with water; b, screen for
head of observer; c, lamp; h, screen extending to ceiling; s, s', screen 25 cm.
high.

The method of experimentation was to place an individual at a
distance of seventy centimeters from the light (where the intensity
was 225 candle-meters) and watch it through a small hole in the screen
b, until a definite movement had taken place. After a reaction of this
kind, the animal was held for a few seconds outside the screen s, where
it could not see the light, in order to eliminate any directive effect
produced by that stimulus, and it was then replaced ready for another
reaction. To counteract the effects of compensatory movements, the
animals were always turned in a clockwise direction between the re-
actions, and were placed with the right and left sides alternately to-
ward the light, the long axis of the body being at right angles to the
direction of the rays. To avoid effects due to fatigue, no more than

twenty reactions were, as a rule, recorded from an individual on any one day. As the method of procedure was the same in all cases, and, as the only object in view was to compare the reactions of eyeless and normal animals, the discussion under each species will be limited mostly to the results obtained.

(c) Amblystoma punctatum.

Four individuals were used in the experiments upon this species. After the eyes had been excised, the two smaller animals, which measured about seven centimeters in length, did not survive more than a day or two. The two adult individuals, however, were apparently little affected by the operation, and one of them lived for forty-seven days after it. The results of the experiments are given in Table I. This species is shown to be negatively phototropic, both

TABLE I.[2]

PHOTIC REACTIONS OF AMBLYSTOMA PUNCTATUM, WITH AND
WITHOUT EYES.

Condition of individuals		Normal			Eyeless	
Direction of movement	+	−	0	+	−	0
Reactions { Number	6	88	10	19	71	32
Per cent	6	84	10	16	58	26

in the normal and eyeless condition. As might be expected, there were more movements without reference to the light after the eyes had been excised, but this may have been due to the effects of the operation. Whether this is true or not, the fact remains that the animals were able to respond negatively to light received through the skin.

(d) Plethodon cinereus erythronotus.

This species manifested the same negative phototropism as the last, when in normal condition, but it did not stand the operations well.

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[2] In the tables which appear throughout this paper the following signs are used: " + " indicates a decided movement toward the light, " − " is used for a similar movement away from the light, and "0" signifies that the individual remained still for fifteen minutes or made a movement without apparent reference to the light.

This may have been due to the small size of the animal, which rendered it less able to withstand the unfavorable conditions in its environment after the eyes had been excised. The reactions summarized in Table II. show that the species was negatively phototropic when in

TABLE II.

PHOTIC REACTIONS OF PLETHODON CINEREUS ERYTHRONOTUS, WITH AND WITHOUT EYES.

Condition of individuals	Normal			Eyeless		
Direction of movement	+	−	0	+	−	0
Reactions { Number	4	30	0	12	9	20
{ Per cent	12	88	0	29	22	49

normal condition. After the eyes had been excised, however, the movements were without apparent reference to the light. This indifference may, nevertheless, have been due to the effects of the operation rather than to lack of photic sensitiveness in the skin.

(e) Diemyctylus viridescens.

Like Plethodon, this species did not stand the operation well and gave no reactions which were manifestly due to light after the eyes had been removed. Ten individuals were used, and the eyes were excised from eight of them. None of the latter lived more than twelve days after the operation. The results given in Table III. bring out the fact

TABLE III.

PHOTIC REACTIONS OF DIEMYCTYLUS VIRIDESCENS, WITH AND WITHOUT EYES.

Condition of individuals	Normal			Eyeless		
Direction of movement	+	−	0	+	−	0
Reactions { Number	242	88	10	30	29	57
{ Per cent	71	26	3	26	25	49

that this species is positively phototropic ; a condition which is not, so far as I know, found in any other caudate amphibian.   All the individuals used were of the orange type of coloration, and it is possible that animals of this species having the green phase might give different results.

(ƒ) Rana clamata.

Although the eyes were not excised from any individual of this species, the reactions observed are given in Table IV. for comparison with

TABLE IV.

PHOTIC REACTIONS OF RANA CLAMATA.

Direction of movement		+	−	0
Reactions	Number	104	37	15
	Per cent	67	23	10

the next form.   They agree essentially with those described by Parker (:03[b]) and Torelle (:03) for R. pipiens and R. viridescens.   Five individuals were tested, and they all proved to be positively phototropic.

(g) Rana sylvatica.

This frog was more active than the last species, and some individuals gave more decided phototropic reactions than did any member of the

TABLE V.

PHOTIC REACTIONS OF RANA SYLVATICA, WITH AND WITHOUT EYES.

Condition of individuals		Normal			Eyeless		
Direction of movement		+	−	0	+	−	0
Individual No. 1		20	0	0	20	0	0
Individual No. 2		17	2	1	10	5	5
Individual No. 3		7	11	12	..	..	..
Individual No. 4		6	7	1	..	..	..
Total Reactions	Number	50	20	14	30	5	5
	Per cent	60	24	16	75	12	12

preceding species.   There were, however, such differences in the re-
actions of the four animals used that they are tabulated separately.
Individual No. 1 never failed to move straight toward the light.   No. 2
was not as persistently positive after the eyes had been excised as be-
fore this operation, though it continued to give a majority of positive
reactions.   As individuals 3 and 4 were apparently indifferent to the
light in their normal conditions, their eyes were not removed.   The
reactions of animals 1 and 2 were, however, strongly positive, and this
condition remained even after the eyes had been excised ; hence their
skins served as photoreceptors as well as their eyes.

(h) Bufo americanus and B. fowleri.

Both these species were used for experimentation, but, as the records
were not kept separate, their reactions cannot be distinguished and
are given together in Table VI.   The results include experiments with

TABLE VI.
PHOTIC REACTIONS OF NORMAL AND EYELESS TOADS.

Condition of individuals	Normal			Eyeless		
Direction of movement	+	−	0	+	−	0
Reactions { Number	802	265	11	126	47	17
{ Per cent	74	25	1	66	25	9

twenty normal animals and six in which the eyes had been excised.   In
removing the eyes from another individual, the head was cut diagonally
so that the left ear was injured.   This animal turned continually to the
right, regardless of the direction of the light, and its reactions were
therefore not included in the table.   Although most of the individuals
were adults, a few were immature, but none of them measured less than
two centimeters in length.   The results show the species to be positively
phototropic in response to stimulation received through the skin as well
as through the eyes.

It was also possible to show that the phototropic reactions of eyeless
toads were not due to the effect of light upon the exposed ends of the
optic nerves.   On two occasions, after an individual had given ten
successive positive responses, it was immediately oriented in such a
manner that the anterior end of the body pointed away from the light.
In both instances the animals turned at once and went directly toward

the light, and this reaction was repeated on five successive trials. These reactions could not have been due to the direct stimulation of the optic nerves by light, as they were not exposed to such stimulation. The results are in agreement with those of Graber ('83), who filled the orbits of Triturus with black wax, and of Dubois ('90), who covered the eyes of Proteus with a mixture of gelatine and lampblack.   Both these observers obtained phototropic reactions by stimulating the skin.

(i) Conclusions.

From the experiments described it may be said that photic sensitiveness is general in the skin of amphibians.   While there is considerable variation in the phototropism of different species, and even of individuals of the same species, the reactions brought about by stimulation through the skin alone are like those produced when both the skin and eyes act as photoreceptors.

B. The Influence of Mechanical Stimulation on the Photic Reactions of the Toad.

In the experiments with terrestrial amphibians and light the observations were always made after the animals had been handled by the experimenter, and, though the response was decided in most cases and of such a nature as to attribute it to light, it is not impossible that mechanical stimulation through handling may have been responsible for more or less of it.   In order to test this matter five toads which were known to be positively phototropic were placed successively in a box, the floor of which measured thirty-eight by ninety centimeters. The sides and floor of this box were of slate, and the ends were closed by glass heat-screens containing a layer of water 3.75 centimeters thick.   The roof consisted of a coarsely woven black cloth stretched on a wooden frame, and the observations were made through the meshes of this cloth.   A lamp giving a light intensity of 220 candle-meters was changed from one end to the other at five-minute intervals for a period of fifteen minutes.   Four of the individuals when first placed in the apparatus went toward the light, and then wandered back and forth without evident reference to it, and apparently tried to escape from the enclosure.   The fifth animal sat in the centre of the box, turning from one side to the other for three minutes, and then went away from the light.   When the lamp was changed from one end of the apparatus to the other, only one of the individuals turned immediately and went toward it; the other four were apparently indifferent. In a later experiment, however, two toads were observed to be persist-

ently positive, and they tried for as much as five minutes to move through a heat screen to the light.

Six toads were next placed together in a rectangular glass vessel (the floor of which measured twelve by twenty centimeters) and were subjected to approximately the same light conditions as in the last experiment. In jumping about they stimulated each other in a mechanical way. During fifteen minutes all the individuals remained mostly facing the light and making vain attempts to reach it, and only occasionally did one of them try to escape on the opposite side of the jar.

It is evident from these two experiments that mechanical stimulation exerts an influence on the phototropism of the toad by enforcing the effect of light, or, it could perhaps better be said, that the mechanical stimulation furnishes the *impulse* to locomotion, while the light is effective in *determining* the direction of the movement after locomotion has been established. For the purpose of the present paper, however, it makes no difference whether the responses obtained were due solely to the influence of light or whether they were reactions to light after mechanical stimulation. In either case the fact remains that both the skin and eyes of amphibians act as photoreceptors, and that definite reactions take place as a result of stimulation through either.

C. The Reactions of the Toad to Photic Stimulation through the Eyes alone.

Experiments have been described in this paper which show that various amphibians react in the same way when either the skin alone is stimulated or when both the skin and eyes are affected. The next question which naturally arises is whether animals will react in the same way when the stimulation is received through the eyes alone. That such responses take place in Rana pipiens has been shown by Parker (:03 [b], p. 33), who found this species to be positively phototropic when its entire surface was covered, with the exception of the eyes. In order to test the toad in a similar manner the apparatus shown in Figure 3 was used. Light was allowed to pass through a small opening (*e*) in a screen, which could be adjusted so that only a small area around the eye of the animal was illuminated. As an additional precaution against light reception through the skin, the individuals used were covered, except the eyes and feet, by a tight-fitting suit of soft leather. As might be expected, the movements of the two animals used in the experiments were slow. Each of these individuals was placed with its right and left side alternately toward the light, the

long axis of the body being at right angles to the direction of the rays. The movements which resulted from this method of stimulation are summarized in Table VII. The results show that the toad gives the
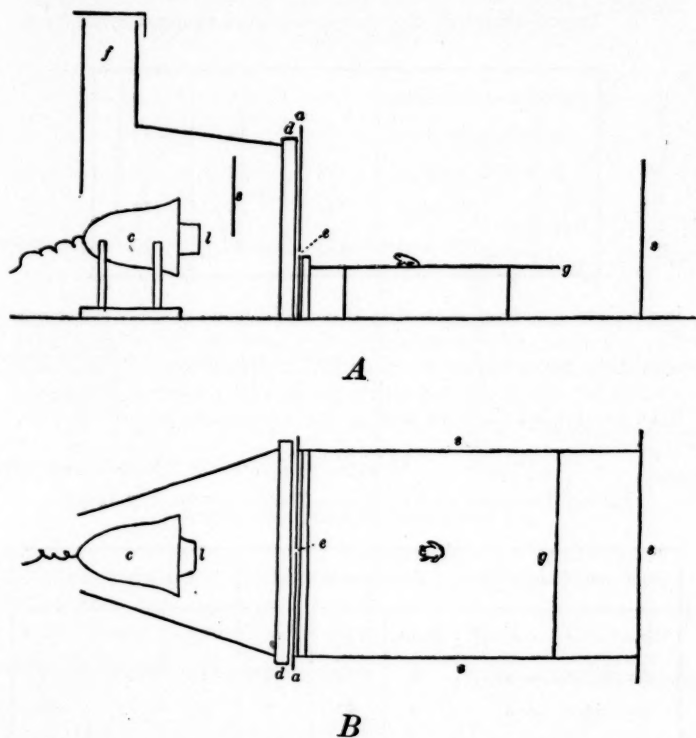
FIGURE 3. *A*, section of apparatus to test reactions of toads to stimulation through the eyes alone; *B*, ground plan. *a*, screen; *c*, lamp; *d*, heat screen; *e*, aperture for light; *f*, chimney for carrying away heat; *g*, slate upon which the animals were placed; *l*, source of light; *s*, screen.

same sort of positive reactions when the eyes are stimulated as when the skin is illuminated.

If the reactions of the two individuals just described were due to unequal stimulation of the eyes, it ought to be possible to produce

circus movements by stimulating only one eye. In order to obtain such unilateral stimulation, a flap was fastened in the leather suit used

TABLE VII.

PHOTIC REACTIONS OF TOADS STIMULATED THROUGH THE EYES ALONE.

Direction of movement		+	−	0
Individual No. 1		73	14	13
Individual No. 2		72	22	6
Reactions	Number	145	36	16
	Per cent	72	18	10

in previous experiments so that it could be made to cover either eye. The individuals were placed so that they faced the light with only the area about the uncovered eye illuminated. Under these circumstances seventy per cent of the movements (Table VIII.) were not toward the light but toward the side bearing the uncovered eye. These reac-

TABLE VIII.

PHOTIC REACTIONS OF TWO TOADS FACING TOWARD THE LIGHT AND STIMULATED THROUGH ONLY ONE EYE.

Condition of individuals		Right eye covered			Left eye covered		
Direction of movement		Right	Left	+	Right	Left	+
Individual No. 3		33	45	22	63	21	16
Individual No. 4		0	97	3	66	5	29
Reactions	Number	33	142	25	139	26	35
	Per cent	17	71	12	69	13	18

tions are what might be expected from a positively phototropic species like the toad, as similar responses have been observed in many other animals. For example, circus movements have been noted in several arthropods after one eye had been blackened over or excised, by Holmes (:01, :05), Parker (:03·), and Rádl (:03). No observations

of exactly this kind have been made on amphibians, although Torelle (:03, p. 474) found that a frog went toward the light with the long axis of the body oblique to the direction of the rays, or made circus movements, after one eye had been covered. She made no attempt, however, to stimulate the eye without also affecting the skin.
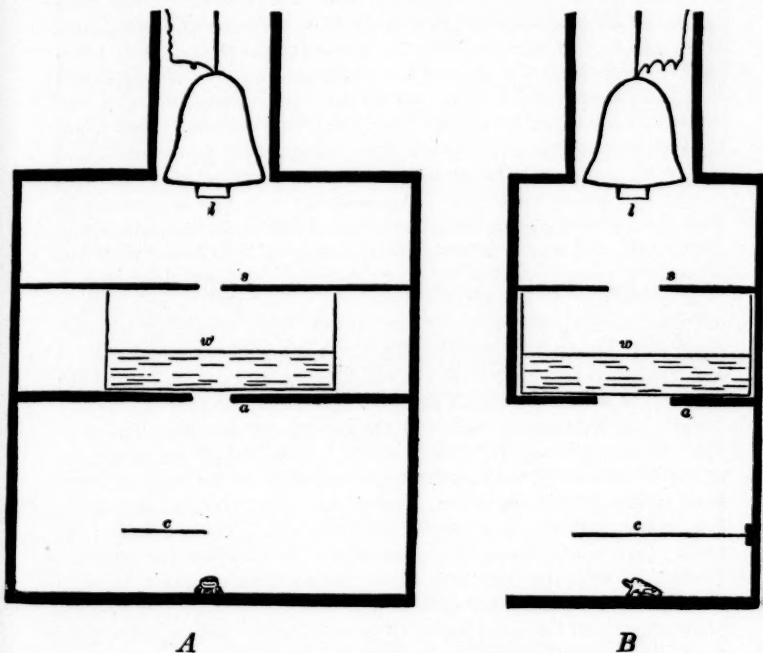
FIGURE 4. A, front sectional view through the middle of the apparatus for testing eyeless frogs under unilateral stimulation; B, sectional view from the side. a, wooden support for heat screen, which contained an oblong opening; c, adjustable screen of blackened sheet iron; l, source of light; s, black cardboard screen; w, glass dish containing water.

From these experiments it is apparent that the photic reactions of the toad, which are brought about by stimulation through the eyes, are due to intensity differences in the illumination of the two eyes, and the direction of the light rays is apparently of no significance.

D. The Reactions of Eyeless Toads to Unilateral Stimulation by Light from above.

The last experiments described showed that a toad would turn toward the illuminated side when only one eye was stimulated, even when such a movement did not take it into a region of greater light intensity. The next question which suggested itself was whether eyeless individuals would make similar movements when only one side was stimulated. In solving this problem, the apparatus shown in Figure 4 was used. It consisted of a wooden box (sixty centimeters high, forty-five wide, and twenty-eight deep) which was lined throughout with two layers of black cloth, except the floor, which was of slate. Light coming from above (l) passed through oblong openings in two screens (a, s) so that an area a little larger than a toad was illuminated on the floor of the apparatus, where the light intensity was 413 candle-meters. Each toad was so placed that the right and left sides were alternately illuminated, and an accurate unilateral division of light and shadow was secured by using a small movable screen (c) of blackened sheet iron.

In preparing individuals for these and subsequent experiments, a different method was used for excising the eyes from that followed heretofore. Instead of removing the whole upper jaw, a horizontal cut was made just above the nostrils, which met a vertical cut behind the eyes. The roof of the mouth was thus left intact, and there was consequently no interference with the respiratory movements. The plan followed in experimenting was to orient the individual facing the observer before each of the first ten reactions, while for the last ten it was faced in the opposite direction. Before and after the tests with light from above, each toad was tested ten times with light of the same intensity (413 candle-meters) from the side. The results of the reactions (Table IX.) with the light from above show a turning toward the side illuminated in seventy per cent of the cases, and, while the positive phototropism of the same individuals was slightly greater when they were illuminated from one side, the difference does not amount to enough to be significant. It may therefore be said that the positive phototropism of eyeless toads is due to intensity differences on the two sides of the body.

Payne (:07) has performed experiments of the same kind with the blind fish, Amblyopsis spelaeus, after the eyes had been excised, and obtained similar results. Apparently the direction of the light rays, as distinguished from intensity differences, has no influence on the reactions of either of these species.

TABLE IX.

REACTIONS OF SIX EYELESS TOADS TO VERTICAL AND
HORIZONTAL LIGHT.

Direction of light	Light from side			Light from above						Light from side		
Regions illuminated				Light on right side			Light on left side					
Direction of movement	+	−	0	+	−	0	+	−	0	+	−	0
Reactions { Number	54	1	5	42	10	8	48	5	7	38	9	13
{ Per cent	90	2	8	70	17	13	80	8	12	62	15	23

E. THE EFFECTS OF ILLUMINATING SMALL AREAS OF SKIN ON EYELESS TOADS.

In order to test the reactions of eyeless toads to local stimulation by light in various regions of the skin, individuals were placed two centimeters behind a screen containing a circular opening 3.2 millimeters in diameter, through which a horizontal beam of light passed. To render the rays of light as nearly parallel as possible a large condensing lens

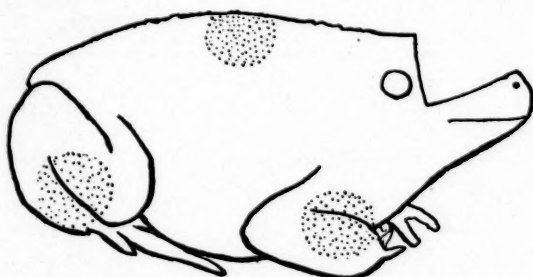FIGURE 5. Toad, viewed from right side. The dotted areas indicate the regions illuminated.

was interposed between the screen and the light. A small area of skin could thus be strongly stimulated by light; the light used had an intensity of 474 candle-meters. The three regions shown by the dotted areas in Figure 5 were stimulated, and they may be designated as the regions of the front leg, the hind leg, and the back. Before each of

the tests the individuals were tried in light of lesser intensity, but applied to the whole surface of the body, to see that they were positively phototropic.

TABLE X.

LOCAL SKIN ILLUMINATION OF EIGHT EYELESS TOADS.

Regions illuminated	Whole body			Front leg			Hind leg			Back		
Direction of movement	+	−	0	+	−	0	+	−	0	+	−	0
Reactions { Number	104	18	20	15	6	5	74	21	21	18	10	4
Per cent	73	13	14	57	23	20	64	18	18	56	31	13

The experiments (Table X.) showed the toad to be positively phototropic in response to stimulation received through each of the regions tried, and there was no reason to assume that one region was more sensitive to such stimulation than another.

TABLE XI.

SUMMARY OF DAILY SERIES OF TWENTY REACTIONS BY ELEVEN TOADS
AFTER PREVIOUS EXPOSURE IN THE LIGHT OR IN THE DARK.

	Previously in dark			Previously in light		
Direction of reaction	+	−	0	+	−	0
First reaction { Number	29	20	6	33	10	3
Per cent	53	36	11	59	17	23
First 5 reactions { Number	188	73	11	174	58	42
Per cent	69	27	4	64	21	15
Last 15 reactions { Number	668	116	5	589	65	9
Per cent	84	15	1	88	10	1
Total reactions { Number	851	179	16	763	121	51
Per cent	81.3	17.1	1.5	81.6	12.9	5.5

Payne (:07) has shown a similar condition in Amblyopsis.   He states (p. 323) that these fishes " seem to be equally sensitive on all parts of

the body," after the eyes have been excised.   Parker (:05ᵇ, p. 419) and
Reese (:06, p. 94) have, on the other hand, found the tail to be the most
sensitive region in Ammocœtes and Cryptobranchus respectively. These
few observations indicate that the comparative sensitiveness of the skin
to photic stimulation varies in different species of vertebrates.

F. The Effect of Previous Conditions of Light Stimulation on
Photic Reactions.

It had been noticed in a general way during the preceding experi-
ments that when a toad was placed near a strong light the first reac-
tion was more often away from the light than any of the subsequent
responses were, and that the first reaction was usually slower than
those which followed. G. Smith (:05) has shown that, when Gam-
marus is exposed to light, a pigment migration takes place toward
the proximal ends of the retinula cells, and that as this migration pro-
gresses the animal changes its reactions from indifferent to strongly
positive. As a pigment migration, as well as other changes, takes
place when the eyes of amphibians are exposed to light, it was thought
that there might be a similar influence on the reactions in this case,
and experiments were accordingly carried out to test this question.

In these experiments toads were placed in the centre of a box which
was ninety centimeters long and thirty-eight wide. The floor and
sides were of slate, and both ends were closed by glass heat-screens
which contained a layer of water 3.75 centimeters thick.   Light, which
had an intensity of 220 candle-meters at the spot where the toads were
exposed to it, was admitted from one end, and before each reaction the
individuals were placed with the right and left sides alternately toward
the source of light.   Eleven toads were kept first in the dark for five
days and then in the light (three candle-meters) of a gas jet for an
equal period of time.   The eyes were thus exposed continuously to
uniform light or dark, except when the animals were removed for the
experiments, which occupied about half an hour daily.   By taking
twenty records from each individual each day, an attempt was made
to get a series of a hundred reactions from each individual under the
two conditions of previous exposure to light and to dark.   In all but
three cases these attempts were successful.

The results in Table XI. show that the first reaction in a series of
twenty has the least tendency to be positively phototropic and that
subsequent reactions are increasingly positive.   There is, however, no
great difference between the responses of individuals previously exposed
to light and those previously in the dark. In Table XII. the reactions

of each animal are shown, and it will be seen that the individuals often vary widely in their different reactions. For example, toad No. 13 was negatively phototropic after being in the dark, but strongly positive after exposure to light. Although the effect of previous stimula-

TABLE XII.

REACTIONS OF INDIVIDUAL TOADS PREVIOUSLY IN THE LIGHT
OR IN THE DARK.

Condition	Previously in dark			Previously in light		
Direction of movement	+	−	0	+	−	0
Individual No. 11	94	6	0	100	0	0
Individual No. 12	89	11	0	76	6	3
Individual No. 13	26	74	0	95	5	0
Individual No. 15	89	10	1	74	9	1
Individual No. 22	94	5	1	82	14	4
Individual No. 23	88	9	3	64	25	7
Individual No. 24	72	8	2	83	14	4
Individual No. 25	97	9	0	64	34	2
Individual No. 26	76	22	2	10	1	18
Individual No. 27	59	8	7	26	3	12
Individual No. 28	73	27	0	89	10	1
Total { Number	851	179	16	763	121	51
reactions { Per cent	81.3	17.1	1.5	81.6	12.9	5.5

tion is marked in some individuals, yet when we consider the total number of reactions, almost the same percentage of positive phototropism is shown after prolonged exposure to the light as after a similar period in the dark. These results agree with those of Torelle (:03), who found that eight hours of exposure to light did not change the positive phototropism of the frog.

Table XIII. shows the times which elapsed before the reactions recorded in Table XII. took place. No records were included which

did not show twenty successive reactions on the day considered. Under (*a*) sixty such sets of daily records are included, and under (*b*), forty-three sets. The toads reacted more slowly after having been kept in the dark than after they had been exposed to light. The difference is not great and cannot be considered very significant in showing optic influence. The results may, however, be interpreted as indicating that prolonged exposure to light renders the toad more photokinetic.

G. The Reactions of Amphibians to Lights of Different Colors.

In testing the reactions of animals to lights of different wave lengths the apparatus shown in Figure 6 was used. Animals were placed in the position shown in the figure, and after each reaction they were rotated clockwise through 180°. The right and left sides were thus brought alternately toward the light, which had an intensity of 612 candle-meters (for white light) at the point where the animals were placed. The different colors were obtained by passing the white light of a Nernst lamp through colored screens. These screens were solutions of various substances held in rectangular glass jars which could be easily interchanged.[3] The colors used were red, yellow, green, and blue, and, though they were not perfectly monochromatic, they did not overlap significantly in the spectrum.

[3] The substances used in making the solutions and the ranges of the colors obtained from them, as determined by an Engelmann spectroscope, were as follows:

Colors.	Substances.	Amount in grams.	c.c. of water.	Wave-length in μ.
Red	Fuchsin	0.10	750	0.605–0.608
Yellow	Potassium bichromate and Copper sulphate	63.00 15.00	750	0.540–0.605
Green	"Lichtgrün" and Copper sulphate	1.50 5.00	750	0.460–0.530
Blue	"Bleu de Lyon"	0.15	750	0.430–0.485

TABLE XIII.

AVERAGE REACTION TIMES IN MINUTES OF TOADS PREVIOUSLY
IN THE LIGHT OR IN THE DARK.

Number of the reaction	1	2	3	4	5	6	7	8	9	10
(a) Previously in dark	8.3	3.5	2.2	2.0	1.8	1.4	1.3	1.1	1.1	1.1
(b) Previously in light	5.9	3.5	3.4	1.6	1.8	1.4	0.8	0.8	0.9	0.8
Number of the reaction	11	12	13	14	15	16	17	18	19	20
(a) Previously in dark	1.1	1.0	1.0	0.9	0.9	1.0	0.8	1.0	0.7	0.8
(b) Previously in light	0.7	0.7	0.6	0.7	0.6	0.7	0.7	0.6	0.5	0.5

(a) *Normal Individuals.*

For the experiments with animals in normal condition, Rana
palustris was used.   Six individuals were successively tested with the
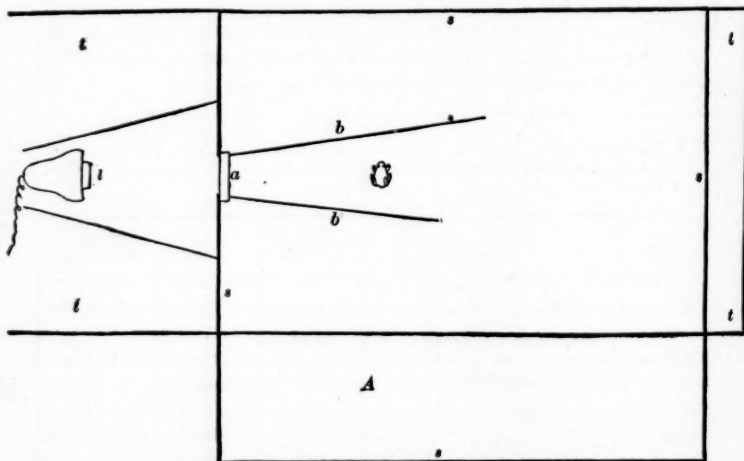colors in the following order, blue, green, yellow, red, and then this

FIGURE 6. Plan of apparatus for testing the reactions of toads to colored
lights. A, position of observer; a, heat and color screen; b, screen 25 cm.
high; l, light; s, s, s, s, screen extending to ceiling; t, t, t, t, table.

order was reversed.   The plan followed was to test all the individuals in one color and then to change the screen and test them again in the same order but with the next color ; ten reactions being taken from each individual in every color.   Each animal was thus actually subject to experiment for about one hour out of the six which were required to complete the series.   A second half-dozen of frogs was tested in the same manner, except that the colors were used in the order red, yellow, green, blue, and then the order was reversed.

TABLE XIV.

REACTIONS OF RANA PALUSTRIS TO COLORED LIGHTS.

Color of lights		Blue			Green			Yellow			Red		
Direction of movement		+	−	0	+	−	0	+	−	0	+	−	0
Reactions	First six individuals	96	13	11	80	14	26	69	20	33	66	16	39
	Second six individuals	81	25	14	68	38	14	55	39	26	45	29	46
	Total { Number	177	38	25	148	52	40	124	59	59	111	45	85
	Total { Per cent	74	16	10	62	22	16	52	24	24	46	19	35
Ave. reaction time in minutes		2.83			3.09			3.60			3.75		

The results (Table XIV.) show that blue is apparently the most effective in the production of positively phototropic reactions, and that there is a regular graduation from blue to red, both in the percentage of positive reactions and in the rapidity with which the movements took place.   Other observers (p. 165) have obtained similar results in experiments with other species of amphibians.   It is probable that these differences in the reactions are due to differences of the wave lengths, but they may be due to intensity differences.

(b) *Eyeless Individuals.*

The blue end of the spectrum is known to be more potent in affecting changes in the eyes of many animals, and in some species the sensitiveness to red is apparently lacking altogether.   For example, Abelsdorff (:00, p. 562) observed that the pupil of the owl's eye

enlarged in red light but contracted rapidly when it was exposed to blue light of low intensity. It therefore seemed not improbable that the differences in the frog's reactions to lights of different colors might have been due to stimulation received through the eyes; therefore another set of experiments was undertaken to ascertain if like results could be obtained through the stimulation of the skin alone.

As toads had been found to be more responsive than frogs after the eyes had been excised, they were used in testing the light reactions through the skin. The same apparatus (Figure 6) was used as in the experiments with normal animals, except that the light was passed through a square aperture, 2.7 centimeters on a side, and had an intensity of 874 candle-meters for white light at the point where the animals were placed. The method used for removing the eyes was the

TABLE XV.

REACTIONS OF THREE EYELESS TOADS TO COLORED LIGHTS.

Color of lights	White			Red			Yellow			Green			Blue		
Direction of movement	+	−	0	+	−	0	+	−	0	+	−	0	+	−	0
Reactions { Number	48	1	1	38	2	10	37	2	11	38	5	7	37	3	10
Per cent	96	2	2	76	4	20	74	4	22	76	10	14	74	6	20

same as in previous experiments (p. 182). Three individuals were tested successively with white, red, yellow, green, and blue light in the order given. The next day two of the animals were tested again with the same colors but in the inverse order.

It will be seen (Table XV.) that these toads gave about seventy-five per cent of positively phototropic reactions with every color. Apparently all the colors were equally effective in inducing photic responses. This fact is the more striking when we remember that the same color screens were used as in the experiments with normal amphibians (Table XIV.), in which case the blue was most potent. The reactions to white light, in the present instance, showed an almost perfect positive phototropism, and it seemed possible that the lesser degree of reactiveness shown in the responses to colored lights might have been due to differences in intensity, as the color-screens undoubtedly cut off much light. To ascertain if any difference would be manifest in the responses if the intensity were lowered, a diaphragm, having a circular aperture 2.8 millimeters in diameter, was interposed and

experiments performed in which eyeless toads were placed at a distance of 275 centimeters from the lamp, where the intensity was 1.44 candle meters for white light.   The colored screens cut the light down to what must have been considerably less than a candle-meter.   The results obtained from seven toads not previously tested are shown in Table XVI.

TABLE XVI.

REACTIONS OF SEVEN EYELESS TOADS TO COLORED LIGHTS OF LOW INTENSITY.

Color of lights	White			Red			Yellow			Green			Blue		
	+	−	0	+	−	0	+	−	0	+	−	0	+	−	0
Direction of movement	+	−	0	+	−	0	+	−	0	+	−	0	+	−	0
Reactions { Number	84	6	10	56	26	28	76	18	16	65	21	24	59	28	25
Per cent	84	6	10	50	23	27	68	17	15	58	19	23	53	25	22

Although the " positive percentages " in every color were lower than when light of greater intensity was used (Table XV.), the eyeless toads again showed positive phototropism in all the colors.   There was also, in this case, a greater number of positive reactions when white light was used than when any of the colors were substituted for it.   It is, then, apparent that in a decreased light intensity the number of positive reactions decreased, but no especial potency was shown by one color as compared with another as a means of inducing such reactions. The slight differences between the number of positive reactions produced by lights of different colors, as shown in the table, may be accounted for as being due to intensity differences.   The colors, as judged by the human eye, could be arranged from more to less intense in the following order, yellow, green, red, blue ; and it will be seen that the largest number of positive reactions was brought about by the most intense light, thus judged.

(c) Summary.

The results of the reactions of amphibians to colored lights may be briefly summarized as follows : normal animals were positively phototropic in all the colors tried, but there were more positive reactions toward the violet end of the spectrum than toward the red end ; eyeless individuals were also positively phototropic in all the colors, but there was no difference in number between the positive reactions to the several colors.   These results do not agree with those of most other observers.

In fact, Loeb ('88) has stated as a general law, that the more primitive the photoreceptor, the greater is its sensitiveness to the rays toward the violet end of the spectrum, as compared to those toward the opposite end.   Graber ('83, p. 225) stated that in the phototropic responses of Triturus the rays became more and more like darkness in their effects as the red end of the spectrum was approached; and that this was true of eyeless individuals as well as those in normal condition.   Dubois ('90, p. 358) observed that blue was more effective than red in producing responses from a blinded Proteus when only the tail was illuminated.   Opposed to these observations are those of Kühne ('78[b], p. 119), who found that, while normal frogs rested in green when there was equal opportunity to rest in blue, blinded individuals showed no such reactions.   The results described in the present paper agree with those of Kühne, and it seems to be evident that the photoreceptors in the skin of the frog and toad have little or no sensitiveness to color differences, as such.

H. Comparison of the Reactions of Eyeless Toads to Heat and to Light.

It has long been known that the skin of amphibians could be stimulated by heat, and the opinion has been expressed that there are receptors which are open to stimulation by either heat or light.   Korányi ('93) showed that heat, as well as light, might produce motor reactions when it was applied to the skin of a frog.   Parker (:03[b], p. 34) says : " It is conceivable that in the lower vertebrates, like the frog, the end organs of the skin are stimulated by radiant energy of a wide range, including what is for us both radiant heat and light, and that the descendants of these organs in the skins of higher vertebrates are more restricted in function and are ordinarily sensitive to radiant heat and its effects."   Washburn (:08, p. 142) also says, " While, then, the nerve endings in the human skin are sensitive only to the slowest of these vibrations, the heat rays, those in the skin of the frog, may respond to the whole series."

During the experiments with eyeless toads the question arose as to whether the supposed photic reactions might not, after all, be due to the influence of heat.   And, although a heat screen containing water was used in all experiments, there was a possibility that the light was converted into heat as it was absorbed by the skin, and that the sensitiveness was to heat rather than light.   Furthermore, the part of the apparatus containing the lamp was warmed somewhat during a series of experiments and gave off a small amount of heat.   A crude test as

to the effect of this heat from the apparatus was made in the following way : On two occasions when a toad had gone successively ten times toward the light, an opaque screen was interposed in such a way that the light was cut off but the radiating heat from the apparatus was allowed to reach the toad. In both instances the individuals gave ten reactions without apparent reference to the heated apparatus, thus showing that the reactions had not been brought about by heat.

In order to test the sensitiveness of the toad to increased temperature, two eyeless individuals were suspended in such a way that the hind legs could be dipped into water. Neither of these animals made any movement under this method of treatment when the water was at room temperature (20° C.). The temperature of the water was then raised five degrees at a time, and there was no response until a temperature of 40° C. to 45° C. had been reached, when the animals quickly withdrew their legs from the hot water. It was evident, from these results, that the toad did not respond *readily* to increase in temperature. Reese (:06) found that Cryptobranchus also was comparatively insensitive to changes in the temperature of the surrounding medium, but, if the temperature was raised above 40° C., violent motor reactions occurred.

While these observations showed that amphibians might not be very sensitive to thermic stimulation, the possibility was not excluded that the assumed photic reactions might in reality be due to stimulation of the skin receptors by heat. If the positively phototropic reactions of blinded toads were due to the stimulation of such receptors, it ought to be possible to obtain similar reactions through the use of radiant heat instead of light. To ascertain if this were possible, an apparatus was arranged in which steam was passed through a vertical brass pipe which measured seven millimeters in diameter. The eyeless toads were placed near this pipe, and their reactions tested in the same manner as had previously been done with light. All these experiments were performed in the dark, but before and after the heat experiments each individual was tested with light (1.24 candle-meters) to ascertain whether it was positively phototropic or not. The method of experimenting in the dark was to orient the toad by using a mark at a known distance from the source of heat; then to listen until a movement was heard; after which the position of the animal was ascertained by feeling for it with the hand. In Table XVII. the signs +, —, and 0 are used to indicate movements in relation to the steam pipe as a source of heat, as they have previously been used for sources of light. As this table shows, toads placed near (10 to 20 cm.)

the heated pipe showed a slight tendency to move away from it, but beyond twenty centimeters they were apparently indifferent.

The amount of heat given off by the steam pipe as compared to that given off by the light apparatus was determined by means of a pair of thermometers. These thermometers were mounted in a wooden box (Figure 7), blackened inside and out and divided into two freely com-

TABLE XVII.

REACTIONS OF FOUR EYELESS TOADS TO LIGHT AND TO RADIANT HEAT.

Nature of stimulation	Light			Distances from a hot pipe, in centimeters														
				10			20			30			40			50		
Direction of movement	+	−	0	+	−	0	+	−	0	+	−	0	+	−	0	+	−	0
Reactions { No.	108	6	16	16	29	5	17	25	8	64	59	27	16	34	10	25	21	14
Reactions { Per ct.	83	5	12	32	58	10	34	50	16	44	40	16	30	54	16	40	34	26

Nature of stimulation	Distances from a hot pipe, in centimeters															Light		
	60			70			80			90			100					
Direction of movement	+	−	0	+	−	0	+	−	0	+	−	0	+	−	0	+	−	0
Reactions { No.	13	9	8	15	14	11	15	13	2	15	11	4	14	18	10	131	21	18
Reactions { Per ct.	42	30	28	38	35	27	50	42	8	50	37	13	34	43	23	77	13	10

municating compartments in each of which the blackened bulb of one of the thermometers (A, B) was enclosed. One of these compartments was permanently closed, while the other could be opened or closed at will by a slide (d). This apparatus was placed in such a position that the radiant heat to be measured fell directly upon the bulb of the thermometer B when the slide was out. After reading the thermometers at intervals and allowing the apparatus to become adjusted to the surroundings for two hours, the difference between the two thermometers was observed at one-minute intervals for twenty minutes while the compartment was open to receive the light or heat to be tested, and then for a like period of time with it closed. The

average difference between the two thermometers, when placed before the steam pipe was 0.064° C. while that for the light apparatus was 0.025° C. The amount of heat received by a thermometer at a distance of thirty centimeters from the heated pipe was therefore more than twice that received when the light apparatus was tested. As the toads were strongly positively phototropic to this light, and as the same individuals were indifferent when placed near the steam pipe, it is safe to conclude that thermo- and photo-reception are distinct processes in the toad's skin, and that, in this animal at least, heat does not give rise to tropic reactions unless there is very strong stimulation.
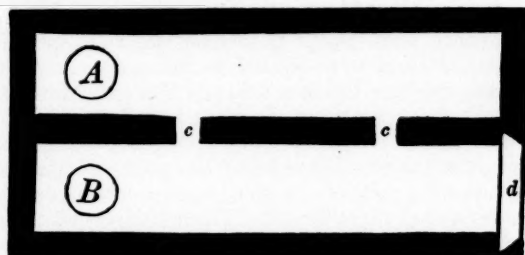

FIGURE 7. Plan of thermometer box. A and B, thermometers; c, c, positions of two of the ten circular openings between the two compartments; d, slide.

I. EXPERIMENTS TO DETERMINE THE INFLUENCE OF THE CENTRAL NERVOUS ORGANS ON THE PHOTIC REACTIONS OF AMPHIBIANS.

Parker (:05[a]) succeeded in obtaining photic responses from one of the lower fishes (Ammocœtes) after the entire brain had been removed, and he believed that such reactions were brought about by stimulation received through skin receptors and transmitted through the spinal nerves. To ascertain if similar reactions could be obtained from amphibians, experiments were undertaken with four species. The first to be tested was Rana pipiens. A sharp scalpel was inserted through the dorsal wall of the cranium and a transverse cut was made through the diencephalon ; this was followed by another cut behind the second vertebra which separated the cord from the myelencephalon. After such individuals had been tested, they were killed and hardened in alcohol. Subsequent dissection showed that the cuts had been successfully made in ten of the twelve individuals upon which operations had

been performed. This method of procedure separated the cord from the brain, but did not interfere with the vital centres in the latter nor with the sympathetic system. These frogs were tested several times, for the two or three days during which they lived, by suspending them at the anterior end in such a way that the hind legs could be subjected to various stimuli. All of these individuals flexed the legs when they were touched with a brush which had been moistened in ten per cent acetic acid, and four of them reacted in the same manner when the light and heat from a Nernst lamp was thrown on the skin, a lens being used to bring the light to a focus; but not a single individual reacted to light from this lamp when the heat rays were cut off by interposing a flat-sided jar filled with water.

Ten toads were tested by the same methods as those used for the frogs, and, though they reacted to acid and the light with heat, no reactions were obtained when light alone was used.

As no photic reactions had been obtained from spinal frogs or toads, it was thought that such responses might be induced if the animals were rendered more sensitive; and experiments were accordingly undertaken in which the diencephalon and cord were transected in nine toads and 0.001 grain of strychnine inserted into the dorsal lymph space through a small slit in the skin. The individuals which had been treated in this manner were extremely sensitive to tactual stimuli, and the slightest jar of the table on which they were supported sufficed to throw their limbs into a state of spasmodic extension. When, however, a beam of light was focussed on the hind leg of such an individual, no indubitable responses were obtained.

Since the attempts to induce photic reactions in terrestrial amphibians had met with no success after the brain had been separated from the cord, I next turned my attention to the available aquatic species. The eyes were removed from a single Cryptobranchus, and its cord was cut behind the first vertebra. This individual was then placed in an aquarium, and light from a Nernst lamp was focussed upon its skin in various regions; and, although it had been found to be extremely responsive to light after the eyes had been removed, no such responses were obtained from it after the cord had been cut. It nevertheless continued to respond to tactual stimulation, and when the side was stroked gently with the finger, it jerked its legs and drew its tail away from the stimulated region. Chemical stimulation was also effective after the cord had been cut, for when a pellet of cotton moistened with ten per cent acetic acid was placed so that it touched the tail, the body was bent away from the stimulated area.

As the experiments with Cryptobranchus had given only negative

results, it was determined to make cuts in various regions of the cord
in different animals and determine whether the individuals thus treated
would show differences in their behavior. The eyes were accordingly
removed from four specimens of Necturus, and the cord was cut behind
the fourth, ninth, eleventh, and twentieth vertebræ in the respective
individuals. All these animals gave marked reactions to light when
the illumination was anterior to the cut in the cord, but no responses
were obtained from the region posterior to this cut, even when a strong
beam of light was focussed on the skin. The regions posterior to the
cut were, however, influenced by certain forms of stimulation, and re-
sponded by making withdrawing movements when they were stroked
with a brush, or when cotton saturated with ten per cent acetic acid
was placed in the water near them. All the individuals seemed to stand
the operation well; the gill movements continued in a normal manner,
and walking was carried on by the front legs, while the posterior part
of the body dragged behind. All these animals lived more than five
days, and one of them (with its cord cut behind the eleventh vertebra)
lived thirty-six. This particular individual was extremely active, and
when the front part of the body was in motion the hind legs also made
walking movements, though they had a slower rate than that of the
front legs. Furthermore, by gently pinching the tail the hind legs
could be induced to walk when the front legs were quiet. In swim-
ming, however, the trunk muscles of the whole body moved together.
Loeb (:03) noted similar correlated swimming movements in Ambly-
stoma larvæ after the cord had been transected. Notwithstanding
such correlated movements, it may be said of the four specimens of
Necturus that the parts of the body in front of and behind the cut
in the cord carried on reactions more or less independently, and that
the regions anterior to this cut responded to a greater range of
stimuli.

As none of the spinal amphibians tested showed sensitiveness to
light, even when reactions were easily induced by other forms of
stimulation, it seems reasonable to conclude that their lack of sensi-
tiveness to photic stimulation was not due to the absence of receptive
or motor power, but to the fact that the ultimate control (centres or
essential portions of reflex arcs) of these reactions lies in the brain and
therefore anterior to the spinal cord.

In order to discover what parts of the brain were essential for the
photic responses, experiments were carried out in which certain regions
were excised and observations made of the deficiency phenomena thus
brought about. The method followed was to excise all parts of the
brain anterior to a certain region, and to carry the regions excised

progressively backward in successive operations; the light reactions being tested at each step. On account of the large size of their brains, Necturus and Cryptobranchus were used for these experiments. The individuals were wrapped in a damp cloth, the head being allowed to protrude; and a T-shaped incision was then made in the skin on the dorsal side of the head, the stem of the T being toward the anterior end; after this the muscles were cut away and the bony roof of the cranial cavity carefully picked away with a pair of strong forceps. The brain was then cut across with a pair of scissors or a sharp scalpel and the parts anterior to the cut removed. The flaps of skin were drawn over the wound and stitched together with silk thread. The success of such operations was verified by subsequent dissection. The method used in testing photic reactions was to throw a vertical band of light (which had an intensity of about 220 candle-meters at the point where the animals were placed) upon the anterior or posterior end of an individual, and to observe the responses which took place. As such responses were like those previously described (p. 169), they need not be discussed in detail.

For a preliminary test as to the effect of such an operation as has just been described, aside from the actual cutting of the brain itself, the roof of the cranial cavities was removed from four individuals and the brain was left exposed to the water in which they were kept. These individuals seemed to be little affected by the operation, as they swam and walked in a normal manner; and when (twenty-four hours later) light was thrown on the anterior or posterior end of any one of them, it reacted in the same manner as an individual in which only the eyes had been excised. The exposure of the brain had, then, no obvious effect on the photic reactions of Necturus.

The eyes and telencephalon were next removed from six individuals, and five of them gave marked responses to light on the day after the operation. The other individual, which lived for fifteen days, gave no photic responses until the third day after the cerebral lobes had been excised, though it had apparently recovered from the operation before that time. These animals could doubtless have been kept alive for a long time if it had not been for the Saprolegnia which grew abundantly around the cut surfaces, and, even with this handicap, one of them lived for fifty days. The cerebral lobes are not, then, essential for the photic reactions of Necturus.

Owing to the scarcity of material, the number of operations had to be limited in the remaining experiments. The portions of the brain anterior to the mesencephalon were, therefore, excised in only one Necturus. This individual lived for twelve days and gave character-

istic reactions when it was touched gently on the foot or tail, or when cotton which had been moistened in ten per cent acetic acid was placed in the water near it. When it was turned on its back, the righting reaction occurred, though this was accomplished with some difficulty. Light, however, called forth no response, even when a condensing lens was used to bring the rays to a focus on the skin. The investigations of Schrader ('87) and Loeser (:05) have demonstrated the fact that the mesencephalon exerts an inhibitory influence on those reflex actions that take place through the spinal nerves. These observers found that frogs were more responsive to external stimulation after the brain had been excised so as to leave only the myelencephalon than when such an operation did not include the mesencephalon. In other words, the midbrain had an inhibitory action on the reflexes controlled by the portions of the brain posterior to it, and when the more anterior brain regions (which originate the "spontaneous" reflexes) had been removed it rendered the frogs unusually sluggish. It is probable that the mesencephalon exerts a similar influence in other amphibians, and that the lack of responsiveness in Necturus was due to inhibition rather than lack of ability to respond to light. The following experiments support this view.

The portions of the brain anterior to the metencephalon were removed in two specimens of Cryptobranchus. Both these individuals were restless and usually continued to move about slowly for some time after locomotion had once been induced by any form of stimulation. When either of them was kept in dim light for an hour or two, however, it became quiet, and, if it was afterwards suddenly illuminated (with light having an intensity of about a thousand candle-meters), there was in most cases an active locomotor response and the movement continued for some time, even after the light had been shut off.

As the metencephalon is poorly developed in all amphibians, and as it has been shown to exert little, if any, influence on their ability to perform locomotor reactions, it is safe to conclude that the myelencephalon and the cord are the only portions of the central nervous system which are essential for the photic responses.

III. DISCUSSION AND CONCLUSIONS.

Photic responsiveness is a quality which is probably present in all amphibians, for the sixteen species which have been found to give reactions to light include representatives of most of the families of the class. Light has an orienting influence on all the species which have been studied; the Caudata are mostly negative in their phototropism,

while the Salientia are positive. Such reactions are easily conceived to be of benefit to the different species under their ordinary conditions of environment, but whether the different types of reactions have arisen as the result of natural selection in the development of each species, or whether they are due to structural peculiarities which limit each species to certain stereotyped reactions and have hence caused it to frequent a particular habitat, or whether they have been brought about by other factors, are open questions. The negatively phototropic reactions of the nocturnal species would serve to bring them into places of concealment during the day. The positive reactions of the more diurnal forms would lead them toward the water (a large illuminated area) and thus facilitate their escape from pursuing enemies, or would take them into the bright sunlight, where insects were abundant and their hunger would be satisfied.

Under artificial conditions light has been shown to have a directive influence on the movements of all the amphibians which have been made the subject of experiment, but it does not follow that the presence of light will *induce* motor reactions in all these species, and there is, in fact, great variation between the different forms in this respect. For example, Cryptobranchus is strongly photokinetic and becomes restless when suddenly illuminated, while Necturus is comparatively indifferent to such stimulation. This photokinetic quality is apparently little developed in frogs and toads, though they are strongly phototropic. Generally speaking, there seems to be no correlation between the photokinesis and the phototropism of amphibians.

A given individual of any species is seldom consistently positive or negative in its phototropism, even when the conditions of light stimulation are uniform. This may be due to the influence of internal factors which bring about changes in the physiological state of the animal, or to external stimuli other than light which exert a modifying influence. Some of these modifying factors will be briefly considered, as far as they apply to the amphibians. Broadly speaking, the habits of the different forms are correlated with their phototropic responses and the species which are most truly terrestrial (Bufo americanus and Rana sylvatica) are most strongly positive, while the typical aquatic forms (Cryptobranchus alleghaniensis and Necturus maculosus) are as decidedly negative. Therefore any variation from the conditions found in the normal habitat of a species might involve changes which would alter its ordinary phototropic responses. Previous exposure in light or dark does not usually exert a marked influence on the photic reactions of the toad, but some individuals were found to be positive after having been in the light, though they were negative after passing

a similar period in the dark.   Mechanical stimulation serves to initiate reactions which are directed by light, but it produces no marked changes in phototropism.   Fatigue makes the photic responses more difficult to induce in some cases (e. g. Cryptobranchus), but does not alter their character.   These few examples are typical and will serve to illustrate the influence of many factors on the photic reactions of amphibians.   In general it may be said that, while various factors may give rise to changed phototropic responses in some individuals, the same factors may be without apparent influence in others.   No stimulus, with the possible exception of decreased temperature (Torelle, :03) has been demonstrated to produce uniform changes in the light responses of amphibians.   The internal causes which produce negative reactions in one species, or even in one individual of a species, while the same external conditions call forth positive reactions in other species or individuals, is practically an untouched field as far as the amphibians are concerned.   The careful study of such a form as Diemyctylus, which undergoes marked changes in habitat during its life, ought to throw light on at least one aspect of this matter.

The next subject that deserves consideration is the nature of the photoreceptors upon which the sensitiveness of amphibians to light depends.   There are at least two sets of nerve terminations which are open to photic stimulation, those of the retina and those of the skin. The investigation of the responses produced by light received through these two sets of endings is involved in considerable difficulty, for we are obliged to refer constantly to judgments formed through the human eye.   We are able to form opinions as to the direction, intensity and color of light, and to judge the form, size, color, position, and movement of illuminated objects as they appear through our own eyes, but we have no conception of how these things appear when they are seen through the eyes of an amphibian, except as we can interpret its actions, and the problem becomes even more difficult when we attempt to consider the reception of light through the skin.   There is some evidence that nervous connections exist in amphibians between these two kinds of photoreceptors and this complicates the matter still farther.   Englemann ('85) observed that retinal changes were induced in the eyes of frogs by illuminating the skin.   Furthermore, Fick ('90) found that the same changes took place after the optic nerves had been cut, and connections, if they exist, must therefore take some other course, in part at least, than that through the second nerve.

The eyes of amphibians are adapted for use in both air and water, and are hence not finely adjusted for visual discrimination in either medium.   Binocular vision cannot be present, as the eyes are placed

laterally, so that there is probably no overlapping in the fields. Nor is any definite image formed, as Beer ('98) has shown that the eye cannot be accommodated to any extent, and amphibians therefore depend upon motion rather than the form of objects to warn them of danger or to enable them to capture food. A frog or toad will allow a worm to lie in full view as long as it is quiet, but as soon as the worm moves it is devoured. The vision of amphibians is therefore limited to rather ill-defined outlines of the surrounding objects, and the comparative brightness or dulness, or possibly the colors, of objects will have considerable importance in determining the nature of the responses of an individual. The reactions brought about when the eyes alone are illuminated are similar to those which take place when such stimulation affects both the skin and eyes. When only one eye is stimulated. by light coming from in front of a toad, the individual usually does not go toward the light but turns toward the stimulated side. These facts indicate that the eyes in their relations to objects in the field of vision serve more as direction eyes than as camera eyes. Cole has recently given additional support to this view by showing that amphibians placed between two lights of equal intensity but of different areas go toward the larger area ; thus demonstrating that the size of the area illuminated is of importance in the visual processes. Kühne ('78ᵃ) has shown that the eye of the frog is sensitive to light rays from the whole range of the visible spectrum, and the results described in the present paper, as well as those of other observers (p. 165), indicate that the rays toward the violet end are most effective in producing photic responses. These apparent differences in sensitiveness to what appear to the human eye as colors may, however, be only differences in intensity when received by the frog's eye.

The skin is known to act as a photoreceptor in ten representative species of amphibians, and individuals show tropic reactions which are like those of animals in normal condition after their eyes have been excised. There is no great differentiation shown in the structure of the nerve endings in amphibians' skins, and Parker (:03ᵇ, p. 34) has already been quoted as saying, " it is conceivable that in the lower vertebrates, like the frog, the end organs of the skin are stimulated by radiant energy of wide range, including what is for us both heat and light." There seems to be no doubt, however, that the amphibian skin is sensitive to light as such, and no tropic responses are induced by radiant heat having the same energy value as the light which does induce marked tropic reactions. Our knowledge of the comparative sensitiveness of the skin in different regions of the body is rather limited, but it shows that there is no uniformity among different am-

phibians in this respect. Cryptobranchus is most responsive when the tail region is illuminated, but the skin of the toad is equally sensitive on all parts of the body.

The fact that both the skin and eyes act as photoreceptors in fishes as well as amphibians has led to considerable speculation concerning the origin of the retina in higher vertebrates. Various theories have been put forward, but only two of them have direct relation to the field included in the present paper. Willem ('91) advanced the view that in its primitive condition light sensitiveness was distributed over the whole skin and that it had become gradually localized in the eyes of higher forms. Parker (:08) has pointed out an objection to this view in the fact that photic sensitiveness is lacking in the skin of the most primitive member of the vertebrate series (Amphioxus), though it possesses direction eyes which are closely connected with the central nervous organs. He believes that the development of photoreceptive power in the skins of vertebrates has been a separate process from that of the development of the retinas, which first arose in intimate connection with the central nervous system. This question cannot be regarded as definitely settled, and the results of the experiments described in the present paper throw little light upon it. The fact that photic sensitiveness is present in such a wide range of amphibians seems to support Willem's view, as the different forms have developed along extremely diverse lines.

Not only do the photoreceptive organs constitute important factors in a consideration of the photic reactions of amphibians, but variations in the light itself are important. Differences in intensity are significant in the reactions of the toad, for the percentage of positively phototropic responses decreases and the number of indifferent reactions increases when the light intensity is decreased. The direction of the incident rays of light which impinge on the photoreceptor is, however, of no apparent consequence. A toad in which only one eye is illuminated by light from in front turns toward the stimulated side instead of going toward the light, and an eyeless toad subjected to unilateral stimulation by light from above turns toward the illuminated side without regard to the direction of the rays. In general, then, the photic reactions of amphibians are brought about by intensity differences on the two sides of the body. Concerning the influence of the quality of the light, it may be said that both the skin and eyes of amphibians are open to stimulation by light rays which include the whole range of the visible spectrum. When the light is received through both the eye and skin receptors, the rays toward the violet end of the spectrum are most effective in producing tropic responses, but when

the light is received through the skin alone, no such potency is shown by the more refrangible rays. The differences observed in the first case may therefore be interpreted as being due to stimulation received through the eyes, and we may conclude that the power of color perception, as distinct from light perception, is present in the eyes but absent in the skin. It is not certain, however, that these differences, which are supposedly due to differences in wave length, are not, after all, brought about by intensity differences.

Generally speaking, the parts of the central nervous system are segmentally arranged throughout the vertebrate series. Each neural segment is, however, capable of carrying on only the comparatively simple reflex actions which are concerned with the somatic segment which it controls. The complex reactions which involve correlated movements in different regions of the body depend upon correlation centres, and, the higher we go in the vertebrate scale, the more these centres become localized toward the anterior end of the nervous tube. A spinal eel is able to swim in a normal manner (Bickell, '97), but in the higher vertebrates spinal reactions show less correlative power, and there is a correspondingly greater importance attached to those reactions which are controlled through the brain. The fact that spinal fishes react to light (Parker, :03b), while spinal amphibians do not, is therefore perhaps to be expected and may be interpreted as new evidence of the progressive anterior localization of functions in the nervous system of vertebrates. However, Sherrington (:06, p. 9) has called attention to the fact that only stimuli of a particular kind will evoke certain reflexes. He was easily able to induce the croak reflex in a spinal frog by certain forms of stimulation, but he could not evoke it by others, and he also found that the scratch reflex could be called forth in spinal dogs by certain forms of tactual stimulation only. It is therefore possible that spinal amphibians may yet be induced to give photic reactions under some new method of stimulation. As far as the present evidence goes, however, the myelencephalon, as well as the cord, is essential for photic responses in which the skin is the receptor.

In the reactions of many organisms the ultimate direction of locomotion is determined by making many random movements and following such of them as lead away from conditions unfavorable to the organism or into conditions better adapted to its existence. Other organisms do not make great use of this method, but usually move directly toward or away from the source of stimulation, and Loeb ('90) has given the name of tropism to such responses. The light reactions of amphibians are characteristically tropic in nature, and, as has been

stated, they are apparently brought about by unequal stimulation on the two sides of the body. This tropic character applies to the reactions whether they are induced by stimulation through the skin or eyes or through the simultaneous stimulation of both. In general, it may be said that the photic responses are of a typically reflex character and show little evidence of powers of association.

IV. SUMMARY.

(1) The following amphibians were found to be positively phototropic: Diemyctylus viridescens, Rana clamata, R. palustris, Bufo fowleri, B. americanus; and the negatively phototropic species studied were: Necturus maculosus, Cryptobranchus allegheniensis, Amblystoma punctatum, Plethodon cinereus erythronotus.

(2) Most of the species mentioned under (1), after the removal of their eyes, gave photic responses which were like those of normal individuals.

(3) The photic reactions of eyeless amphibians are not due to the direct stimulation of the central nervous system or the exposed ends of the optic nerves by light, but to the action of the skin as a photoreceptor.

(4) Mechanical stimulation (handling) does not change the character of the photic reactions, though it makes them more evident by inducing locomotion.

(5) Toads which are stimulated by light through the eyes alone react in the same manner as individuals stimulated through the skin or through both the skin and the eyes.

(6) The movements of eyeless toads stimulated unilaterally by light from above are toward the illuminated side; and toads stimulated through one eye only by light from in front do not go toward the light but turn toward the illuminated side. The photic reactions are therefore due to differences in light intensity on the two sides of the body and the direction of the rays is ineffective.

(7) After the eyes have been removed, Cryptobranchus and Necturus are most responsive when the tail is illuminated, but the skin of the toad is apparently of equal sensitiveness on all parts of the body.

(8) A prolonged period of time passed in light or dark had no effect on the nature of the phototropic responses of the toad.

(9) Cryptobranchus is strongly photokinetic, but in the other amphibians tested this quality was not strongly developed.

(10) When normal amphibians were used, blue light was the most effective in the production of tropic responses, but when eyeless indi-

viduals were tested with the same colored lights, the rays toward the blue end of the spectrum showed no such potency as compared with those nearer the opposite end. It may be said that, while both the skin and eyes are sensitive to the whole range of the visible spectrum, color sensitiveness is present only in the latter. It is possible, however, that the supposed color sensitiveness is due to the effects of what are intensity differences to the amphibian eye.

(11) A decrease in the intensity of the light brings about a correspondingly smaller number of positively phototropic responses and an increase in the number of indifferent reactions.

(12) The phototropic responses of eyeless toads are not due to the stimulation of heat-receiving organs in the skin. Thermo- and photo-reception are separate processes, and the former does not readily give rise to tropic reactions.

(13) Spinal amphibians gave no photic responses, but such reactions were induced in animals in which the brain anterior to the metencephalon had been excised.

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